

CAUTION, WEBS IN THE WAY! POSSIBLE FUNCTIONS OF SILK STABILIMENTA IN *GASTERACANTHA CANCRIFORMIS* (ARANEAE, ARANEIDAE)

Rodolfo Jaffé¹, William Eberhard², Carlos De Angelo³, Diana Eusse⁴, Adrián Gutierrez⁵, Sandra Quijas⁶, Antonio Rodríguez⁷ and Mayanin Rodríguez⁸:

¹Institut für Biologie, Martin-Luther-Universität Halle-Wittenberg, Hoher Weg 4, # 125, D-06099 Halle/Saale, Germany. E-mail: rodolfo.jaffe@zoologie.uni-halle.de;

²Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, San José, Costa Rica; ³Fundación Vida Silvestre Argentina, Iguazú, Argentina; ⁴Universidad del Valle, Cali, Colombia; ⁵Universidad Autónoma de México, México, D.F., Mexico; ⁶Centro de Investigación en Ecosistemas, Universidad Autónoma de México, Yucatán, México; ⁷Grupo de Ecología de Vertebrados, Facultad de Biología, Universidad de la Habana, La Habana, Cuba; ⁸Universidad de los Andes, Mérida, Venezuela.

ABSTRACT. We tested three hypotheses concerning the function of stabilimenta in the orb weaver *Gasteracantha cancriformis*: 1) warning to large animals that might accidentally destroy the web; 2) prey attraction; and 3) camouflage. One prediction of the warning hypothesis (but not of the others), that less exposed webs should have fewer stabilimentum tufts, was verified: very few tufts occurred on the peripheral lines of small webs. On the other hand, a prediction of the prey attraction hypothesis, that webs with more stabilimentum tufts should also have more captured prey, was only confirmed in one sub sample, and further analysis indicated that spider size rather than number of stabilimentum tufts best explained the presence of prey. An additional observation not in accord with prey attraction was that resting webs, which lacked sticky silk for prey capture, nevertheless had abundant stabilimentum tufts. Finally, the number of stabilimentum tufts was lower in the webs of white (as opposed to yellow or orange) spiders, contradicting a prediction of the camouflage hypothesis. The strongest conclusions from our results are support for the warning function, and lack of support for the prey attraction function.

RESUMEN. Pusimos a prueba tres hipótesis concernientes a la función de los estabilimentos en la araña *Gasteracantha cancriformis*: 1) advertencia a animales grandes que podrían destruir accidentalmente la red; 2) atracción de presas; y 3) camuflaje. Se cumplió una predicción de la hipótesis de advertencia (pero no de las demás) de que las redes menos expuestas deberían presentar menos estabilimentos: se observaron muy pocos estabilimentos en las líneas periféricas de redes pequeñas. Por otra parte, la predicción de la hipótesis de atracción de presas, de que redes con más estabilimentos deberían presentar más presas capturadas, sólo se cumplió en una submuestra y análisis posteriores mostraron que el tamaño de la araña y no el número de estabilimentos explicó mejor la presencia de presas. Otra observación que no apoya la hipótesis de atracción de presas fue haber encontrado redes de descanso, las cuales carecieron de un espiral de captura, con un importante número de estabilimentos. Finalmente, el número de estabilimentos fue menor en las redes de arañas blancas (en relación a las amarillas o las anaranjadas), contradiciendo la predicción de la hipótesis de camuflaje. Nuestros resultados apoyan la hipótesis de advertencia y no la de atracción de presas.

Keywords: orb webs, silk stabilimenta, spiders, warning, prey attraction, camouflage

The function of silk stabilimenta on the webs of diurnal orb-weaving spiders has long been debated (e.g., Hingston 1927; Marson 1947; Marples 1969; Edmunds 1986) and remains controversial (see summary by Her-

berstein et al. 2000; Eberhard 2003). The hypotheses which are currently best supported include prey attraction, camouflage from predators, and web advertisement to warn off large animals which might damage the web (several

other hypothesized functions, such as providing shade for the spider, a path for the male to find the female, physical stabilization of the web, and a deposit of excess silk have little support at present). Most of the recent debate regarding silk stabilimentum function has centered on the stabilimenta in the genus *Argiope*, but silk stabilimenta have also evolved independently in several other lineages of orb weavers (Scharff and Coddington 1997; Herberstein et al. 2000). Evidence from other groups is likely to be useful in understanding possible functions.

The araneid orb weaver *Gasteracantha cancriformis* (Linnaeus 1767) is widespread in the New World, ranging from the southern USA to northern Argentina (Levi 1978). Bright body colors have been said to attract prey in another species of *Gasteracantha* (Hauber 2002). It is highly variable in color and shape (Levi 1978). The orbs of mature females of *G. cancriformis* occur in fairly open situations, up to more than 6 m above the ground, and are relatively large: anchor lines extend up to 2–4 m from the hub to supports, and the diameter of the area covered by the viscid spiral can be up to 0.6 m (Marples 1967; Muma 1971).

Stabilimenta apparently evolved independently in this group (Gasteracanthini) from other araneids such as *Argiope* (Herberstein et al. 2000). The stabilimenta on *G. cancriformis* webs consist of multiple short tufts of white silk. Most tufts are on the frame and anchor lines, though they also occur on one or more radii near the hub (Comstock 1967; Marples 1967; Muma 1971; Levi 1978). Tufts of stabilimentum silk are added to frame and anchor lines while the spider is reinforcing a line already in place (Marples 1967); the spider pauses, pulls a loose swath of white silk from its spinnerets with strokes of its hind legs, dabs its spinnerets to the line one or more times to attach the swath, and then moves on. Each tuft consists of many fine threads. Newly made stabilimentum tufts blow out to the side of the main thread in the wind (thus indicating that the lines in the tufts are under no stress, and unlikely to provide any physical support for the web). The stabilimentum silk tends to stick to or entangle itself with the line, and becomes less conspicuous as time goes by (Marples 1967). Marples (1967) noted that sometimes when a spider lacks a “complete”

web (presumably an orb with a sticky spiral) it rests at a central point where several threads bearing tufts converge. Comstock (1967) speculated that the tufts of *G. cancriformis* might deceive midge-eating insects, which in their efforts to capture the supposed midges accidentally fly into the web. Muma (1971) stated (probably somewhat imprecisely, as will be shown below) that the “webs of immatures are different from those of sub-adult or adult females in lacking . . . distinct tufts of silk on the radii or foundation lines . . .”

In this note we test predictions made by each of the three major hypotheses for stabilimentum function. The warning hypothesis (but not the others) predicts that stabilimentum tufts should be more abundant in orbs which are larger and span larger spaces, and are thus under greater risk of being destroyed by large animals passing by. The fact that birds have been seen to actively avoid orb webs (Blackledge & Wenzel 1999), and that birds which have flown through spider webs show signs of intense discomfort, immediately preening themselves extensively (Robinson & Robinson 1976), support the assumption of this hypothesis that visual signals from spiders or their webs might be used by birds to avoid webs. The prey attraction hypothesis (but not the others) predicts that spiders with more stabilimenta should be more often found feeding on prey. Finally, the camouflage hypothesis (but not the others) predicts that spiders whose abdomens are white and which thus match the color of the stabilimenta (in contrast to yellow or orange, colors which also occur in the same population), should produce more stabilimenta.

METHODS

On 20 January 2004 (early dry season) in a plantation of African oil palm (*Elaeis guineensis*) located near Parrita, Costa Rica, we followed transects defined by lines of palm trees, covering an area of about 1500 m². We measured the following variables in easily accessible spider webs (approximately 1–2.5 m above the ground): 1) Spider size: estimated by multiplying the length (cephalothorax plus abdomen) by the maximum width of the abdomen (mm); 2) Maximum radius of the viscid spiral: the maximum distance between the center of the hub and the outer border of the viscid spiral; 3) Maximum span of the web:

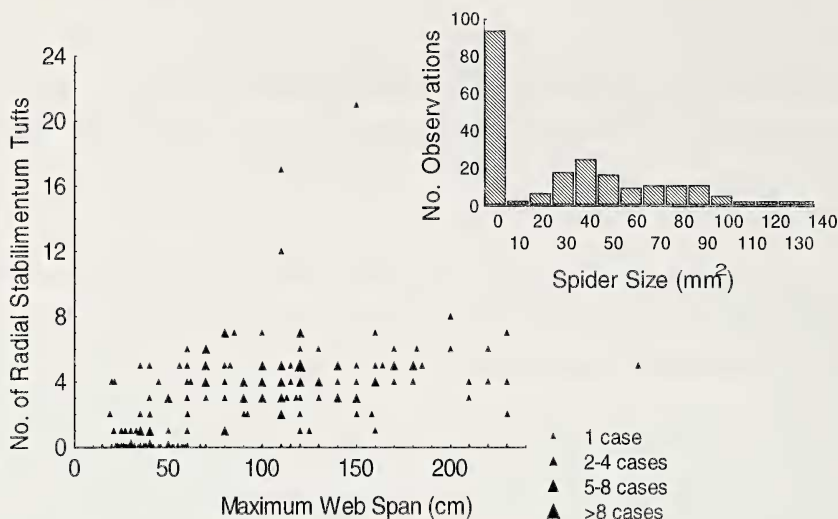


Figure 1.—Number of radial stabilimentum tufts in relation to the maximum web span. The frequency histogram at the upper right shows the distribution of spider sizes ($n = 220$).

the maximum distance between points where anchor lines were attached to the substrate; 4) Number of radial stabilimentum tufts: the number of tufts of silk on radial lines inside the viscid spiral; 5) Number of peripheral stabilimentum tufts: the number of tufts of silk on peripheral and anchor lines, i.e. all tufts outside the viscid spiral; 6) Prey: silk-wrapped prey near the hub; and 7) Color: the color of the dorsal surface of the abdomen, classified as white, yellow or orange. Although there was a certain overlap in some colors, like light yellows, it was relatively easy to assign all spiders to one of these three categories. We measured 220 capture webs with spiders, and in addition, 7 resting webs that lacked viscid spirals.

RESULTS

Warning Hypothesis.—As predicted, smaller webs had smaller numbers of stabilimentum tufts. The numbers of radial and peripheral stabilimentum tufts were positively correlated with both the maximum viscid spiral radius (R 's = 0.70 and 0.77 respectively; $P < 0.001$ in both cases; $n = 218$) and maximum span of the web (R 's = 0.62 and 0.76 respectively; $P < 0.001$ in both cases; $n = 220$) (Figs. 1, 2). Similarly, webs that completely lacked peripheral stabilimentum tufts were smaller than those that had them (3.6 ± 2.0 cm vs. 11.3 ± 4.7 cm for maximum radius of viscid spiral; 43.6 ± 24.2 cm vs. $111.0 \pm$

54.9 cm for maximum span; Mann-Whitney U-Test: $U = 1008$ and 1232 respectively; $P < 0.001$ in both cases; $n_1 = 71$, $n_2 = 147$).

Interpretation of these patterns is complicated by the correlations between spider size and web size, and thus the possibility of indirect effects. Small spiders had fewer radial and peripheral stabilimentum tufts than large spiders (Mann-Whitney U-tests: $U = 894$ and 424 respectively; $P < 0.01$ in both cases; $n_1 = 94$, $n_2 = 126$). Smaller spiders were also more likely to not have any stabilimentum tufts (median = 0 for both radial and peripheral tufts; min-max = 0–5 and 0–30 respectively), while the large spiders typically had a few radial stabilimentum tufts, and a larger number of peripheral stabilimentum tufts (median = 4 and 24.5; min-max = 0–21 and 0–62 respectively).

The agreement with the predictions of the warning hypothesis was not due, however, to secondary effects of the correlation between web size and spider size. When we performed partial correlations of the total number of stabilimentum tufts with the maximum span of the web, the maximum radius of the viscid spiral, and spider size, the maximum span had the highest correlation coefficient ($R = 0.35$, 0.25 , and 0.16 respectively; $t_{214} = 5.51$, 3.81 , and 2.42 respectively; $P < 0.01$ in all cases).

Prey Attraction Hypothesis.—In general, spiders with prey in their webs had higher

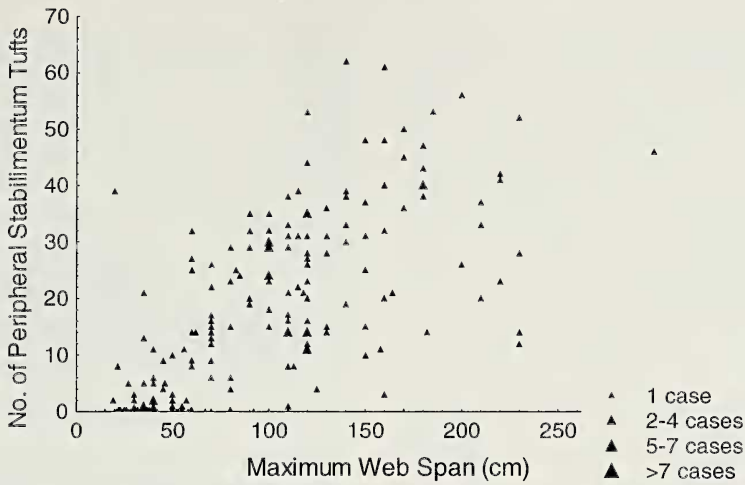


Figure 2.—Number of peripheral stabilimentum tufts in relation to the maximum web span.

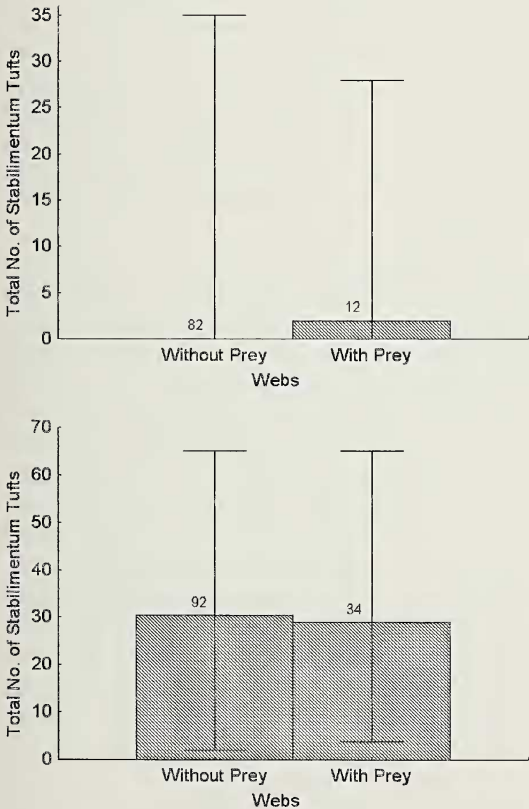


Figure 3.—The median numbers of stabilimentum tufts in webs of small (<15 mm²) and large spiders (>15 mm²) with and without prey (minimum and maximum values are represented by whiskers). Sample sizes are above the columns.

numbers of radial and peripheral stabilimentum tufts than spiders without prey in their webs (Mann-Whitney U-test: $U = 3222$ and 2939 ; $P = 0.036$ and 0.005 respectively). Because the array of potential prey is probably different for small and large spiders, and because the distribution of spider sizes (inset in Fig. 1) suggested the separation of spiders in two size categories (small < 15 mm², and large > 15 mm²), we repeated this analysis separately for both categories.

When the webs of small spiders with prey were compared with those of small spiders without prey, the number of radial stabilimentum tufts was not different (Mann-Whitney U-test: $U = 392$; $P = 0.26$), but the numbers of both peripheral and total stabilimentum tufts were higher in webs with prey ($U = 269$ and 272 , respectively; $P = 0.01$ in both cases; $n_1 = 12$, $n_2 = 82$). On the contrary, in large spiders the numbers of radial, peripheral and total stabilimentum tufts did not vary between webs with and without prey ($U = 1508$, 1538 and 1556 ; $P = 0.76$, 0.88 and 0.97 , respectively; $n_1 = 34$, $n_2 = 92$) (Fig. 3).

The higher number of prey in the webs of small spiders that had more stabilimentum tufts could have been an indirect effect of the relationship between the number of stabilimentum tufts and web size (which is likely to affect capture success) (see Figs. 1, 2), or between stabilimentum tufts and spider size (which is proportional to both web size and to the strength of silk lines (Craig 1987)) (Fig. 4) rather than to the stabilimenta themselves.

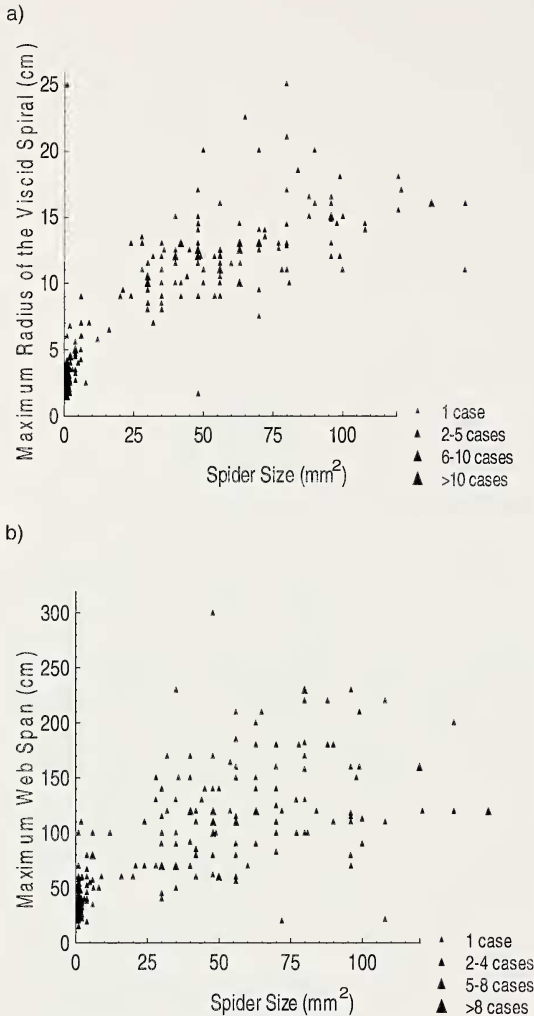


Figure 4.—Relation between maximum radius of the viscid spiral (a) and maximum web span (b) with spider size ($R_s = 0.86$ and 0.78 respectively; $P < 0.001$ in both cases; $n_a = 218$, $n_b = 220$).

In an effort to separate these possible effects, we performed a logistic regression using presence/absence of prey as the response variable, and the number of radial stabilimentum tufts, the number of peripheral stabilimentum tufts, spider size, maximum radius of the viscid spiral, and maximum span of the web as the independent variables. In small spiders, the spider size was the only variable to explain prey presence (Final loss = 33.23; $X^2 = 5.3$ and $P = 0.021$), while in large spiders prey presence was not explained by any of the variables.

We also found seven spiders (44.3 ± 34 mm² in size) on "resting" webs. These were relatively small (maximum span 72.1 ± 30

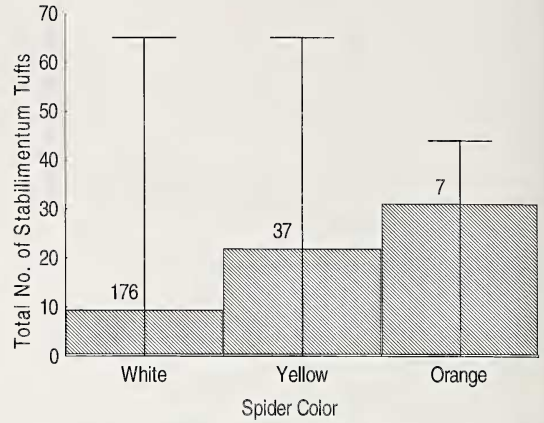


Figure 5.—Median numbers of stabilimenta in webs of spiders with different colors (minimum and maximum values are represented by whiskers). Sample sizes are above the columns.

cm), had few radii, and completely lacked viscid spirals. Contrary to expectations of the prey attraction hypothesis, they all had many stabilimentum tufts (23.4 ± 17.1). In these resting webs, the number of stabilimentum tufts did not correlate with spider size ($R_s = 0$; $P = 1$), or the maximum span of the web ($R_s = 0.36$; $P = 0.42$). Spider size was also not related to the span of the web ($R_s = 0.53$; $P = 0.22$).

Camouflage Hypothesis.—The number of radial stabilimentum tufts did not vary among differently colored spiders (Kruskal Wallis (KW) test: $H_{(2,220)} = 5.1$; $P = 0.078$). Contrary to the prediction of the camouflage hypothesis, the number of peripheral and total stabilimentum tufts was lower in white spiders than in yellow or orange individuals (KW: $H_{(2,220)} = 10.4$ and 9.1 ; $P = 0.005$ and 0.010 respectively) (Fig. 5). Smaller spiders were more likely to be white, so we repeated this analysis for small and large spiders separately. This eliminated all significant differences with respect to spider color (small KW: $H_{(2,94)} = 0.9$; 0.9 and 0.6 ; $P = 0.64$; 0.64 and 0.75 respectively; large KW: $H_{(2,126)} = 1.3$; 1.4 and 1.0 ; $P = 0.52$; 0.51 and 0.60 respectively).

DISCUSSION

Warning Hypothesis.—The strong positive correlations of the number of stabilimentum tufts with the maximum web span and the viscid spiral radius are in accord with the prediction of the advertisement hypothesis. Her-

berstein et al. (2000) claimed that the warning function is unlikely in the stabilimenta of *Gasteracantha* because the spiders build their webs in "shrubs and understory where birds are unlikely to fly through and damage the web" (p. 665). Both our observations and those of previous authors (Comstock 1967; Marples 1967; Muma 1971) show that this characterization of *G. cancriformis* web sites is incorrect. Nor is it likely to be true for the African *Gasteracantha* species (*G. curvispina*) that builds apparently similar stabilimenta and on which they apparently based their description (they cite it in their table as building "under bushes"). The complete description from the reference they cite for this species (Edmunds & Edmunds 1986) is "The web was spun in open spaces, between or under bushes, or attached to buildings" (p. 78).

It is worth noting that the number of peripheral stabilimentum tufts increased approximately linearly with maximum web span (Fig. 2). Use of such a linear increase rule may be the mechanism by which spiders produced the adjustment in numbers of stabilimentum tufts in larger webs that was predicted by the warning hypothesis. In contrast, radial stabilimentum tufts differed in being generally lower in number and in increasing less sharply with web size (Fig. 1). If stabilimenta serve as warning devices, the peripheral stabilimentum tufts may mark the edges of the area occupied by the web, while the radial stabilimentum tufts may simply mark which side of the well-marked periphery of the web is to be avoided (because it has the dense array of radial and sticky lines). This could explain the lower numbers of radial stabilimentum tufts and their weaker relation to web size that were observed.

It is also interesting that the stronger and stickier silk lines of larger spiders that a bird would contact if it flew into an orb are probably more disturbing than the silk lines of smaller spiders, as they may be more restrictive and more difficult to clean off. So, if birds learn from experiences with webs and distinguish those made by spiders of different sizes, larger spiders should gain a greater advantage from having peripheral stabilimentum tufts. This gives a second reason under the warning hypothesis for expecting more stabilimentum tufts on the webs of larger spiders, such as we found.

Prey Attraction Hypothesis.—Our results give little support for the prey attraction hypothesis. First, given that all spiders need to feed, under this hypothesis all spiders should present stabilimenta. The fact that the majority of small spiders did not have stabilimenta in their webs is not easily explained by the prey attraction hypothesis unless *ad hoc* modifications are added. For instance, the prey attraction hypothesis could explain the reduction of stabilimenta in small webs if the prey utilized by large spiders but not by small spiders are attracted to stabilimenta, or if the cost-benefit balance (cost of predator attraction vs. benefit of prey attraction) is different for small vs. large spiders. We know of no evidence favoring these ideas, nor do we know of any data suggesting that they are incorrect.

Second, we did not find the expected relation between prey and number of stabilimentum tufts. In webs of larger spiders there was no significant relation. In small spiders we found the predicted correlation between higher numbers of peripheral stabilimentum tufts and prey, but when the analysis took into account the possibility of indirect influences of other variables, the only variable that explained prey presence was spider size. This implies that the effect on prey attributed to the number of stabilimentum tufts in small spiders may have been due to a relation between prey capture and spider size. It is important to note, however, that the arrival of prey is probably highly stochastic, so larger sample sizes than ours might be needed to document prey capture effects.

A third, especially strong type of evidence against the prey attraction hypothesis comes from resting webs. These lacked viscid spirals, and thus did not function to capture prey, but were nevertheless well equipped with stabilimentum tufts. Stabilimenta were also observed on webs that were apparently of this type by Marples (1967). These resting webs strongly suggest that stabilimenta are not used to attract prey. If these webs serve as molting platforms (one newly molted individual was observed with its shed cuticle on one of these webs, Eberhard pers. comm.), the presence of stabilimenta even on these relatively small webs could be explained by the warning hypothesis. The impact of a large animal might be especially dangerous to a spider in its relatively defenseless condition around the time

of molting. This consideration makes the presence of well developed stabilimenta on resting webs even more difficult to explain under the prey attraction hypothesis, as the impact of prey could also be dangerous for the spider. The prey attraction hypothesis could be saved from these problems by *ad hoc* adjustments (e.g. the stabilimenta on resting webs are selectively disadvantageous "mistakes" by the spider).

Camouflage Hypothesis.—Our data did not support the camouflage hypothesis, nor did they speak strongly against it. The prediction was that the white stabilimentum tufts should have been more abundant in the webs of those individuals that were more likely to be confused with them (white spiders). The lower number of stabilimentum tufts in webs of white spiders contradicts this prediction. However, the logic of this test depends on the spider's ability to adjust its behavior in terms of its own color. Even though some thomisids may be capable of this type of adjustment (Foelix 1996), we know of no case in which an araneid has been shown to be able to sense its own color. This test also depends on the colors detectable by potential predators; for some animals the white silk tufts may appear different from the white coloration of the spider. Because of these uncertainties, we conclude that our data do not justify a certain rejection of this hypothesis.

The camouflage hypothesis might explain the reduction of stabilimenta in small webs, if large but not small spiders have predators that are fooled by stabilimenta. We know of no evidence that supports this possibility. The only predator of *G. cancriformis* that we documented was the wasp *Sceliphron* sp. (Sphecidae). One nest had 3–4 cells full of adult and subadult *G. cancriformis* females. The camouflage hypothesis is compatible with the presence of stabilimenta on resting webs.

In summary, the strongest conclusions from our evidence support for the warning hypothesis, and rejection of the prey attraction hypothesis. Future studies addressing web destruction frequency and prey capture success could help test these conclusions.

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